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Climate effects on prey vulnerability modify expectations of predator responses to short- and long-term climate fluctuations

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27 **1 Abstract**

28 Climate changes affect the distribution and abundance of organisms, often via changes in species
29 interactions. Most animals experience predation, and a number of models have investigated how
30 climate fluctuations can influence predator-prey dynamics by affecting prey abundance through
31 changes in resource availability. However, field studies have shown that prey vulnerability is a key
32 feature determining the outcome of predator-prey interactions, which also varies with climatic
33 conditions, *via* changes in prey body condition or in habitat characteristics (e.g. vegetation cover). In
34 this theoretical work, we explore, with large mammals of African savannas in mind, how the interplay
35 between climate-induced changes in prey abundance and climate-induced changes in prey vulnerability
36 affects the immediate and long-term responses of predator populations. We account for prey body
37 condition and habitat effects on prey vulnerability to predation. We show that predictions on how
38 predator abundance responds to climate fluctuations differ depending on how climate influences prey
39 vulnerability (habitat characteristics vs. prey body condition). We discuss how species traits influence
40 the relative importance of the different sources of vulnerability. For example, our results suggest that
41 populations of cursorial predators (such as spotted hyaenas) are expected to fare better than populations
42 of ambush predators (such as African lions) in African ecosystems that will be characterized by an
43 aridification. This study highlights the importance of understanding, and accounting for, the
44 vulnerability factors associated to a given predator-prey pair, and improves our comprehension of
45 predator-prey relationships in a changing climate.

46 2 Introduction

47 The Earth's climate is changing rapidly, largely because of human activities (IPCC 2014a).
48 Temperature is rising globally and will continue to do so, precipitation regimes are, or will be, locally
49 altered, and extreme climatic events will become more common (IPCC 2014a). Climate changes
50 already have ecological impacts and are, or will soon be, a major driver of species dynamics and
51 survival (Maclean & Wilson, 2011; Pacifici et al., 2017). So far, most studies on the impacts of climate
52 changes have focused on describing changes in population distribution and abundance (e.g. Martay et
53 al., 2017; Parmesan et al., 1999), phenology and demography (e.g. Inouye et al., 2000; Moyes et al.,
54 2011) or behaviour (Candolin & Wong, 2012). Even though these changes can sometimes emerge from
55 the direct effect of climate on individuals, they often result from cascading effects occurring through
56 biotic interactions, such as trophic interactions (e.g. Visser et al., 2006). Therefore, understanding how
57 climate changes will affect species through their biotic interactions is fundamental to grasp the full
58 picture of the impacts of climate changes.

59 Climate changes have the potential to modify predator-prey interactions, which are central in the
60 functioning of populations, communities and ultimately ecosystems (Bastille-Rousseau et al., 2018).
61 First, by altering primary production quality and quantity, climatic conditions influence the body
62 condition of large mammalian herbivores (rainfall: Bourgarel et al., 2002; Owen-Smith, 2002, NAO:
63 Mysterud et al., 2001; snow: Saether & Gravem, 1988). Herbivore body condition, in turn, influences
64 demographic parameters, such as survival (Bender et al., 2007) or fecundity (Cook et al., 2004), which
65 ultimately affect herbivore population abundance. As a result, climate indirectly influences prey
66 abundance through density-dependent processes (Forchhammer et al., 1998; Saether, 1997). For
67 example, several studies linked rainfall to herbivore abundance in savanna ecosystems (East, 1984;
68 Ogutu et al., 2008), or showed the influence of climatic variations on the dynamics of several
69 populations of Northern ungulates (Forchhammer et al., 1998; Post & Stenseth, 1999). Extreme
70 climatic conditions also affect herbivore demographic parameters and ultimately population
71 abundances (e.g. drought: Foley et al., 2008; Mduma et al., 1999). These changes in herbivore
72 abundance originating from climate fluctuations will affect predator populations, as the maintenance
73 of predator populations largely depends on prey abundance (East, 1984; Carbone & Gittleman, 2002).
74 Prey body condition is thus a first pathway through which climate changes may alter predator-prey
75 interactions and such climate-driven impact on prey demography has already been taken into account
76 in pioneering predator-prey modelling works (e.g. Wilmers et al., 2007a; blue arrows in Fig. 1).

77 Predator-prey relationships are also influenced by prey vulnerability, which may arise from
78 intrinsic (inherent to the prey) or extrinsic (arising from the environment) sources. Prey body condition
79 is typically an intrinsic factor that can determine prey vulnerability to predators. Indeed, several studies
80 pointed out that predators tend to select the weakest individuals among prey, and that prey in poorer
81 body condition are more likely to be preyed upon (in savanna ecosystems: FitzGibbon & Fanshawe,
82 1989; Pole et al., 2004; in temperate ecosystems: Atwood et al., 2007; Husseman et al., 2003). On the
83 other hand, habitat characteristics are extrinsic factors that can modulate prey vulnerability to their
84 predators and that can be influenced by climatic conditions. Several studies stressed out the importance
85 of vegetation structure and cover, which interact with the predator hunting technique and the prey
86 escape technique to ultimately affect the hunting outcome. This was shown in savanna (Funston et al.,
87 2001; Hopcraft et al., 2005) and temperate ecosystems (Husseman et al., 2003, Lone et al., 2014). Other
88 habitat characteristics can interfere with the predator hunting success. For example, prey were either
89 more vulnerable to predators with increasing amount of snow (Mech et al., 1971; Post et al., 1999) or
90 less vulnerable to predators as snow hardness decreased (Stenseth et al., 2004).

91 Hence, the true prey availability to predators results from the interplay between prey abundance
92 and prey vulnerability, which is characterized by different sources of vulnerability (red arrows in Fig.

1). Little is known on the relative importance of climate-induced changes on the different components of prey availability to predators, and particularly on the different sources of prey vulnerability. Here, we integrate both prey abundance and vulnerability effects (Fig. 1) in a theoretical study investigating the immediate response of predator populations to a year of a specific climatic condition, as well as the long-term response of predator populations to changes in average climatic conditions. This study aims at providing general insights on the interplay between climate-induced changes in prey abundance and prey vulnerability. The model is, on purpose, not designed for a specific predator-prey system, so that people studying predator-prey interactions worldwide can adapt the model to fit the system there are interested in. However, we designed our study with large mammalian herbivores and carnivores of African savannas in mind so that the parameters and the functional relationships used are easy to relate to a real world. Annual rainfall is expected to decrease in southern Africa and increase in eastern Africa, and generally to become more variable (IPCC, 2014b). We therefore specifically focused on the influence of rainfall conditions on predator-prey interactions in African savanna ecosystems. We modelled the population dynamics of a predator preying on a density-dependent age-structured prey population following the model described in Wilmsers et al. (2007a, b), but we further and originally accounted for prey body condition and environmental effects on prey vulnerability to predation (Fig. 1).

3 Materials and methods

3.1 The predator-prey model

3.1.1 The prey population model without predation

We considered a female-only prey population (Caswell, 2001) which, in any year t , had a total population size of $N(t)$ made of $J(t)$ juveniles and $A(t)$ adults. Fluctuations from year to year were driven by survival and reproduction of individuals, which are now described.

Body condition is a critical individual characteristic, as it links environmental conditions to demography. For simplicity, we assumed a linear relationship between body condition and survival, and thus only modelled the latter. We modelled the effect of body condition on reproduction using a relationship between the probability to reproduce and the probability of survival. Each year, individual survival probabilities $p_{ji}(t)$ and $p_{ai}(t)$, for juveniles and adults respectively, were drawn from Beta distributions with shape parameters α_j and β_j and α_a and β_a for juvenile and adult prey respectively, and differed from one individual to another, allowing to integrate individual heterogeneity. However, new probabilities were drawn each year and were not preserved through the individual's life, and thus varied randomly within individuals from year to year. The method-of-moments gives:

$$\alpha_j = p_j \left(\frac{p_j(1-p_j)}{Sd_{p_j}^2} - 1 \right) \quad (1a)$$

$$\beta_j = (1 - p_j) \left(\frac{p_j(1-p_j)}{Sd_{p_j}^2} - 1 \right) \quad (1b)$$

for juvenile prey, and

$$\alpha_a = p_a \left(\frac{p_a(1-p_a)}{Sd_{p_a}^2} - 1 \right) \quad (1c)$$

$$\beta_a = (1 - p_a) \left(\frac{p_a (1 - p_a)}{Sd_{pa}^2} - 1 \right) \quad (1d)$$

for adult prey, where p_j and p_a are mean survival rates and Sd_{pj} and Sd_{pa} are standard deviations for juvenile and adult prey population respectively. In any year t , mean survival rates p_j and p_a were:

$$p_j(t) = P_j \times g_j(t) \quad (2a)$$

$$p_a(t) = P_a \times g_a(t) \quad (2b)$$

where P_j and P_a are parameters defining the maximum survival rates for juveniles and adults respectively (see Table 1 for all default values of model parameters), and g_j and g_a are scaling functions allowing to account for density- and resource-dependence in survival. These scaling functions (bounded between 0 and 1) are those used by Wilmers et al. (2007b) and follow:

$$g(N(t)) = \frac{\gamma^\delta}{\gamma^\delta + \frac{N(t)}{R}} \quad (3)$$

where R is the annual rainfall of the site. R varied from 300mm to 900mm by 100 mm increment, which are coherent values for annual rainfall in African savannas (Sankaran et al., 2005; Chamailé-Jammes & Fritz, 2009). We assumed that rainfall determined directly and linearly prey resource availability (Rutherford, 1980). We thus considered rainfall as a proxy of the resource availability and the ratio $N(t)/R$ as a number of individuals sharing the amount of available resource for year t . The half-saturation parameter γ determined the per capita resource availability at which the maximum survival rate was reduced by half. Finally, δ was a shape parameter setting the beginning and the strength of the density-dependence (as in Wilmers et al., 2007b).

Juvenile survival is expected to be the first demographic parameter affected by increasing density, followed by age at first reproduction, reproductive success and finally adult survival (Eberhardt, 1977). This hypothesis has found support in large ungulate studies (Bonenfant et al., 2009). As our model was conceptualized for large mammals (as for the one of Wilmers et al., 2007b), we assumed a greater sensitivity of juvenile survival to increasing density by assuming that γ_j was lower than γ_a .

In summary, both rainfall R and population size N determined g and ultimately the average survival rates p_j and p_a in the population (Fig. 2A). Once mean survival probability had been computed, we determined the fate of each individual by randomly drawing a value from a uniform distribution on the [0-1] interval, and comparing it to the individual's survival probability. If the value was lower than the survival probability, the individual survived; if not, it died.

We assumed that juveniles became adults in one year (a realistic assumption for some herbivore species; Estes, 1991) and only adults were able to reproduce. Therefore, the number of juveniles at the beginning of a given year depended only on the fecundity of adults the year before. We also considered that, for each adult, the probability of reproducing (P_f) was a function of its survival probability $p_{ai}(t)$, and the link between P_f and $p_{ai}(t)$ was as follows:

$$P_f(p_{ai}(t)) = \frac{1}{1 + f_{low} \times e^{-f_{growth} \times p_{ai}(t)}} \quad (4)$$

where f_{low} is a parameter determining the probability of reproduction P_f of individuals whose survival probability is close to 0 and f_{growth} a parameter defining the speed at which P_f reaches the value of 1 with increasing p_{ai} (Fig. 2B). We compared, for each individual, values drawn randomly from a uniform

distribution on the [0-1] interval with their reproduction probability. If the value was lower than the reproduction probability, the individual produced one offspring; if not, it did not reproduce.

3.1.2 Integrating predation into the prey model

We modelled an unstructured predator population (similarly to Wilmers et al., 2007a), which, in any year t , had a total population size of $Y(t)$. Predator population dynamics resulted from the combination of a functional response, which describes how the intake rate of a predator varies with prey abundance (Abrams & Ginzburg, 2000; Holling, 1959), and a numerical response, which relates predator intake to changes in its abundance (Bayliss & Choquenot, 2002).

We integrated the influence of prey body condition by accounting for the fact that only adult prey in poor condition, i.e. with a low survival probability, were vulnerable to predators, whereas all juvenile prey were vulnerable to predators, irrespectively of their body condition. To do so, we defined a threshold of survival probability Th . Any adult prey with an individual survival probability $p_{ai}(t)$ below this threshold was integrated to the pool of adult prey vulnerable to predators A_{vuln} . Rainfall and prey density both affected $g_a(t)$ and thus $p_a(t)$, the mean survival probability within the population. Consequently, they played a crucial role in determining the proportion of adult prey in poor body condition. As $p_a(t)$ decreased, there were more adult prey with low individual survival probabilities, and therefore more adult prey with a survival probability under the vulnerability threshold and exposed to predation.

We integrated the influence of habitat characteristics that could affect prey vulnerability through the manipulation of the handling time h , which is classically defined as the time needed by a predator to subdue and consume a prey and during which the predator cannot capture another prey (Abrams & Ginzburg, 2000). In our model, this time to subdue one prey corresponded to all predation attempts (with one predation attempt being a predation sequence: search, encounter, and attack) leading to a successful prey capture. For African savannas, we assumed that an increase in annual rainfall leads to a greater vegetation cover (taller grass, more leaves in bushes and trees) and hence better concealment opportunities for predators to approach their prey undetected (Hopcraft et al., 2005). Hence, we considered that an increase in the climatic variable R would increase prey vulnerability, and consequently decrease the number of attempts leading to a successful attack, i.e. lead to lower handling time h values (an alternate situation where handling time increases with rainfall is presented in the Appendix A of the Supplementary material). Therefore, h varied with rainfall according to the following equation:

$$H(R) = h_{min} + \frac{h_{max} - h_{min}}{1 + e^{B(R-V)}} \quad (5)$$

with $H(R)$ the value of handling time for a given year t and the rainfall value R , h_{min} is the lowest value of h , h_{max} is the maximum value of h , B is the maximum rate of change, V is the rainfall value at which the rate of change of h is maximum (or inflexion point). This equation allowed the handling time to vary non-linearly and negatively with rainfall (Fig. 2C). One value of h was calculated for each rainfall value and was then incorporated into the functional response $I(t)$.

For the functional response, we assumed that the number of prey killed and consumed by one predator during a given year t followed a type II Beddington-DeAngelis functional response. This equation allows the integration of interference between predators when searching for and capturing prey and is formulated as follows:

$$I(P(t), Y(t)) = \frac{\mu P(t)}{1 + \tau Y(t) + \mu h P(t)} \quad (6)$$

where $P(t)$ is the number of vulnerable prey, $Y(t)$ the number of predators, μ a parameter defining the encounter rate between predators and their prey, h the parameter defining the handling time and τ the interference between predators (Abrams & Ginzburg, 2000). Finally, this type of functional response allows both prey and predator densities to impact predators' intake and therefore the regulation of predator populations.

Predation occurs all year around. Consequently, to account for the depletion of prey that occurred throughout the year and could affect the estimation of the number of prey actually captured, we recursively applied the functional response presented in (6) over daily time steps, adjusting prey number at each time step. We named $M(t)$ the total number of prey killed by predators and calculated it as follows:

$$M(t) = P(t) - \sum_{d=1}^{365} I(P(d)Y(t)) \quad (7)$$

where $P(t)$ is the number of vulnerable prey to predation, $P(d)$ the pool of prey vulnerable to predation at the beginning of day d and $Y(t)$ the number of predators at the beginning of year t .

The numbers of juvenile and adult prey killed by a given predator during a year are given by:

$$M_j(t) = M(t) \times \frac{J(t)}{P(t)} \quad (8)$$

$$M_a(t) = M(t) - M_j(t) \quad (9)$$

The $M_j(t)$ juveniles killed in year t were randomly removed from the $J(t)$ juveniles present at the beginning of the year t . Similarly, the $M_a(t)$ adults killed in year t were randomly removed from the pool of vulnerable adults A_{vuln} , i.e. individuals whose survival probabilities were below the threshold of survival probability Th . For simplification, we assumed that adult and juvenile prey were equally profitable to predators. Similar assumption can be found in other modelling studies (e.g. Wilmers et al. 2007a).

Finally, the predator numerical response was given by:

$$Y(t + 1) = \lambda_{max} \times P_{rel}(t) \times Y(t) \quad (10)$$

where $Y(t)$ is the number of predators present in year t , λ_{max} is the maximum growth rate of the predator population and $P_{rel}(t)$ was calculated as follows:

$$P_{rel}(M(t), Y(t)) = \frac{M(t)}{\frac{1}{h_{min}} \times 365 \times Y(t)} \quad (11)$$

with h_{min} the smallest value possible for the handling time. P_{rel} was therefore bounded between 0 and 1 and quantified predators hunting efficiency over a year by expressing the amount of prey actually eaten in year t as a proportion of the maximum amount of prey that predators could have eaten.

3.2 Simulations

To study how climatic conditions may impact predator populations through their influence on prey body condition or habitat characteristics, we designed 4 scenarios:

Scenario 1: climatic conditions influence prey availability through their effect on prey body condition and ultimately on prey abundance. Prey vulnerability to predators did not vary with prey body condition (all prey were vulnerable to predators) nor with habitat characteristics. Climatic conditions therefore influenced predator-prey interactions only through their impacts on prey survival and fecundity, i.e. through prey abundance only (blue arrows in Fig. 1). This demographic effect of climate is present in all scenarios.

Scenario 2: prey vulnerability was affected by climatic conditions through their influence on prey body condition (red arrows in Fig. 1). The poorer a prey body condition, the more vulnerable to predators the prey was. Therefore, climatic conditions influence prey availability through their effect on prey body condition affecting both abundance and prey vulnerability to predation.

Scenario 3: prey vulnerability was affected by climatic conditions through climate-driven changes in habitat characteristics (e.g. vegetation) (red arrows in Fig. 1). Therefore, climatic conditions influence prey availability through their effect on prey body condition affecting prey abundance and on habitat characteristics affecting prey vulnerability to predation

Scenario 4: prey vulnerability was affected by both prey body condition and climate-driven changes in habitat characteristics. In this scenario combining scenarios 2 and 3, climatic conditions influence prey availability through their effect on prey body condition and habitat characteristic and, ultimately, prey abundance and vulnerability to predation.

While in scenarios 1 and 3 predators could capture any prey individual, in scenarios 2 and 4 predators could capture any juvenile, but could only subdue adult prey that were in poor body condition. These differences between scenarios were modelled by setting the value of the threshold of survival probability Th at 1 in scenario 1 and 3, and at 0.5 in scenario 2 and 4 (Table 1). As vulnerability to predators was independent from habitat characteristics in scenarios 1 and 2, the handling time was set constant and equal to $h = 5$ in these scenarios. In scenarios 3 and 4, prey vulnerability to predators was dependent on habitat characteristics and handling time h varied with climatic conditions following equation 5 (for a summary of the model functioning see Fig. 3).

We focused on these 4 scenarios only, as the goal of this study was to assess how the addition of prey vulnerability to traditional predator-prey models that considered prey abundance only would change the expectations in terms of responses of predator populations to climatic changes.

For simulations, parameters were given default values considered realistic for African large mammals. These default values and initial values for state variables are presented Table 1. The sensitivity of the main results to some of these parameter values was investigated by sensitivity analyses (see section below). As we were mostly interested in how the link between climatic conditions and prey vulnerability could affect predator dynamics, predators were characterized by identical parameter values in the different scenarios, but for the threshold Th and handling time h values. Therefore, in our work, all differences in predator dynamics between scenarios emerged from differences in these two parameters.

3.2.1 Immediate response of predator populations to specific rainfall conditions

We assessed, for each scenario, the immediate response of the predator population to specific rainfall conditions. We simulated over 198 years the dynamics of the predator population under the long-term annual rainfall 600 mm, then imposed a predefined rainfall in year 199 (different values were tested: from 300mm to 900mm, by 100mm increments), and calculated the predator population growth rate over that year (calculated as $\lambda = Y_{t+1}/Y_t$). To obtain robust estimates of predator population growth rates and account for within-simulation variability in prey demographic rates, each simulation, characterized by a long-term annual rainfall value of 600mm and one predefined rainfall for the last year, was replicated 1000 times.

3.2.2 Long-term response of predator populations to changes in mean annual rainfall

We assessed, for each scenario, how a change in mean annual rainfall may affect predator populations on the long run. We compared the average predator population size (over the last twenty-one years of a 200-year simulation) across simulations run under different long-term rainfall averages. The mean annual rainfall values varied from 300mm to 900mm, by 100mm increments. For each value, simulations were replicated 1000 times, allowing again to account for within simulation variability in prey demographic rates.

3.2.3 Sensitivity analyses

Because model outcomes can be sensitive to the choice of parameter values, we conducted sensitivity analyses for some model parameters. We first investigated the effect of changes in parameter h_{min} and Th , which are of importance because differences between scenarios originate from these two parameters. In addition, we also tested for the influence of changes in λ_{max} values, which is a central parameter of the predator numerical response. Finally, we carried out a sensitivity analysis for the δ parameter, which describes the shape of density dependence and determines the magnitude of the prey population response, the number of individuals per resource units, and ultimately prey dynamics. We always varied this parameter simultaneously for adult and juvenile, ensuring that juvenile survival never exceeded adult survival (see Fig. 2A). Sensitivity analyses were conducted by increasing or decreasing each of these parameters, one at a time, by 20 percent around its default value. For each parameter value, simulations were replicated 500 times. Results of the sensitivity analyses are presented in the Appendix B of the Supplementary Material.

An example of the behaviour of the model for one run showing fluctuations of rainfall, prey and predator population size over 200 years is presented in Fig. S7 (Appendix C of the Supplementary Material) and a summary of the key steps of the modelling process and of the different scenarios can be found in Fig. 3. All simulations were conducted in R 4.0.2 (R Core Team, 2020).

4 Results

4.1 Immediate response of predator populations to specific rainfall conditions

In scenario 1, i.e. when climatic conditions influenced prey abundance only (through survival and fecundity) and not prey vulnerability, the population growth rate of predators was not influenced by the specific climatic condition of the year (Fig. 4A). This result was not surprising as according to the model design, the demographic consequences of climate are expected to be visible in prey population the following year ($t+1$) and, therefore, would only impact predator growth rate calculated over the year $t+1$ and $t+2$. In contrast, in the three other scenarios, i.e. when climatic conditions influenced prey vulnerability, either through changes in prey body condition (scenario 2) or through changes in habitat characteristics (scenario 3) or both (scenario 4), the population growth rate of predators one year was influenced by the specific climatic condition of the year. Population growth rates in scenarios 2 and 3 showed opposite patterns (Fig. 4A). Predators from scenario 2 benefited from below-average rainfall (600mm) and their populations increased, as shown by the growth rate being greater than 1, but there was a negative effect of above-average rainfall (Fig. 4A). In scenario 3, there was a negative effect of below-average rainfall and a positive effect of above-average rainfall on predator growth rate (Fig. 4A). Because scenario 4 is a combination of scenarios 2 and 3, the population growth rate of predators from scenario 4 was intermediate between those of scenarios 2 and 3 (Fig. 4A).

4.2 Long-term response of predator populations to changes in mean annual rainfall

Our results showed an effect of mean annual rainfall on the size of predator populations for all scenarios, but the shape of the relationships varied. In scenario 1 (when climatic conditions influenced prey abundance only), the size of predator populations increased near-linearly with rainfall (Fig. 4B). As expected because all individuals were vulnerable to predation, the size of predator populations in this scenario was always greater than the one observed in other scenarios. The size of predator populations in scenario 2 (when climatic conditions influenced prey vulnerability through changes in prey body condition only) also increased near-linearly with mean annual rainfall. It was consistently lower than the size of the predator population in scenario 1 because only a fraction of the prey population is vulnerable to predation in scenario 2. However, the effect of climatic conditions on predator population sizes was weaker in scenario 2 than in scenario 1: as the amount of rainfall increased, the difference between scenarios 1 and 2 in the size of predator populations increased (Fig. 4B). Conversely, the size of predator populations varied non-linearly with increasing rainfall in scenario 3, when climatic conditions influenced prey vulnerability through changes in habitat characteristics only, and in scenario 4, when climatic conditions influenced prey vulnerability through both changes in prey body condition and habitat characteristics. More specifically, the size of predator populations in scenario 3 were smaller than those from scenario 2 up until mean annual rainfall reached values around 600mm, but were greater for values above (Fig. 4B). In addition, for mean annual rainfall of 900mm, the size of predator populations in scenario 1 and 3 were almost equal. In scenario 4, changes in the size of predator populations with increasing mean annual rainfall generally followed a similar pattern than those observed from the scenario 3. However, the difference in the size of predator populations between scenario 4 and 3 increased with increasing rainfall (Fig. 4B). Conversely, the size of predator populations were virtually identical between scenario 4 and 2 at the wettest end of the rainfall gradient (Fig. 4B). In all cases, the size of predator populations in scenario 4 was always equal or lower than in the other scenarios (Fig. 4B).

5 Discussion

Our work shows how predator populations could respond differently to changing climatic conditions depending on how climate influences prey vulnerability (habitat characteristics vs. body condition). For example, in a context of aridification, a predator-prey system where prey vulnerability depends mainly on prey body condition (scenario 2) would be characterized by larger predator populations than a system where prey vulnerability is mainly affected by the habitat (scenario 3) (see section 5.1 for the role of species traits). It thus highlights the importance of having a good understanding of the processes determining vulnerability at play within the predator-prey pair studied, as integrating climate influence on prey vulnerability, in addition to resource-mediated climate effects on prey abundance, leads to different responses of predator populations (on the short- and the long-term) to changes in climatic conditions.

5.1 How species traits influence the relative importance of the different sources of vulnerability

Ultimately, whether the predator-prey pair studied will respond according to one scenario or another will depend upon the traits of the species involved. Here, we will illustrate the importance of the predator hunting mode and the prey escape tactics, as well as the importance of the relative size of the predator and the prey. Predator hunting mode (cursorial or ambush) and prey escape tactics (fleeing, fighting or freezing) are key behavioural traits involved in predator-prey interactions that can affect how climatic conditions contribute, indirectly *via* forage resources or vegetation cover, to determine the vulnerability of prey to predation. For example, cursorial predators, such as spotted hyaenas *Crocuta crocuta* (Cooper, 1990) and wild dogs *Lycaon pictus* (Pole et al., 2004) in African savannas,

or wolves in temperate ecosystems (Mech et al., 2015), are active predators, i.e. they can chase down their prey over long distances and are more likely to kill individuals in poor body condition. They therefore exemplify predators from scenario 2 (climatic conditions influence prey vulnerability through changes in prey body condition only), as prey in poorer condition because of a shortage of food will be particularly more vulnerable to predation from these predators (Atwood et al., 2007; Mills, 1995; Pole et al., 2004). Conversely, ambush predators, such as African lions *Panthera leo* and leopards *Panthera pardus* in African savannas, or cougars *Puma concolor* and lynx *Lynx lynx* in temperate ecosystems, stalk their prey before attacking them by surprise when they come within short distance (Elliott et al., 1977; Husseman et al., 2003). As such, they rely less on prey body condition. However, to approach their prey undetected, ambush predators need concealment. Therefore, their hunting success is prone to be influenced by vegetation (Funston et al., 2001; Lone et al., 2014), and negatively affected by an increased aridity and a subsequent decrease in vegetation density (scenario 3, climatic conditions influence prey vulnerability through changes in habitat characteristics only). Whereas prey escape tactics might not be that crucial for the outcome of an encounter with an ambush predator, a climate-driven decrease in prey body condition will negatively influence prey fleeing capacity leading to an overall disadvantage against cursorial predators (scenario 2).

Predator body size influences the prey body size targeted by the predator (Owen-Smith & Mills, 2008a; Radloff & du Toit, 2004) and climate-driven changes in prey body condition can interfere with the chance of successfully subduing an adult prey depending on the relative size of the predator and the prey considered (Mech et al., 2001; Metz et al., 2012). For example, for lion-impala interactions, it is very likely that climatic conditions will not affect the likelihood of lions to capture an adult impala *Aepyceros melampus*, while in the case of lion-buffalo *Syncerus caffer* interactions, lions are expected to successfully hunt adult buffaloes, which are dangerous prey for them, in dry conditions only (scenario 2, Owen-Smith, 2008). This is also true at the interspecific level: prey species that are usually inaccessible because they are too difficult to be captured under normal climatic conditions may become vulnerable due to unfavourable conditions, allowing predators to kill young individuals of larger species (e.g. with elephants: Loveridge et al., 2006; Salnicki et al., 2001).

5.2 Importance of integrating climate-driven changes in prey vulnerability

Our results show how predator population responses to changes in climatic conditions differ when we take into account climate-driven changes in prey vulnerability in addition to climate-driven changes in prey abundance (existing work take into account climate-driven changes in prey abundance only – Fig. 1). For example, while the overall trend depicted in all 4 scenarios on the long-term is that there are more predators when rainfall increases, because of an overall increase in prey population abundance, the originality of our study is to illustrate how prey vulnerability and its drivers influence the link between predator populations and climate.

When changes in climatic conditions influence prey vulnerability through changes in prey body condition (scenario 2), a below average rainfall event leads to poorer herbivore body condition, and hence results in an increase in the pool of adult prey vulnerable to predators (Fig. S8A). Unsurprisingly, this, in turn, favours the immediate growth rate of the predator population. This result is in accordance with field observations, which reported a positive effect of drought conditions over the short-term on large carnivore populations (Mills, 1995). These dry-condition increases in prey vulnerability can be assimilated to “resource pulses” for the predators and to be beneficial to them (Holt, 2008; Yang et al., 2008). Contrarily, above average rainfall events negatively affects the population growth rate of predators, as very few prey adults are vulnerable in years characterized by high levels of resources (Fig. S8A). Over the long term, predator populations benefit from the overall increase in prey populations associated with increasing rainfall (Fig. S9). However, predators in scenario 2 can only

subdue a portion of adult prey and have a smaller pool of available prey than predators in scenario 1. They are therefore maintained at smaller population size. In addition, the proportion of vulnerable adult prey decreases with increasing rainfall (Fig. S8B), which leads to the observed increase in the difference between the size of predator populations in scenario 1 and 2.

When changes in climatic conditions influence prey vulnerability through changes in habitat characteristics and habitat-driven hunting success increases with rainfall (scenario 3), predator growth rates are negatively impacted by below average rainfall and positively influenced by above average rainfall. This is typically the case in African savannas where grass height is related to rainfall (Rutherford, 1980) and lions are hunters that are more successful in tall grass (Funston et al., 2001). Over the long term, predator populations benefit from the combined linear increase of prey abundance (Fig. S9) and non-linear increase of hunting success (i.e. decrease of handling time, Fig. 2C), leading to an overall non-linear increase as rainfall increases.

Finally, when changes in climatic conditions influence prey vulnerability through changes in both prey body condition and habitat characteristics (scenario 4), the growth rate of predator populations combines the effects of both sources of vulnerability and predators are affected by opposite effects of different sources of vulnerability. For below average rainfall, predators benefit from the positive effect of lower prey body conditions, which buffers the negative effect of a lower hunting success due to habitat characteristics, and inversely for above rainfall level, leading to the observed intermediate pattern of predator growth rate (Fig. 4A, Fig. 2C, Fig. S8A). Over the long term, predator populations of scenario 4 follow the same patterns as the populations in scenario 3 with the exception that they can only subdue a proportion of adult prey. They subsequently remain at a smaller population size.

5.3 Contrasting predator responses to short- and long-term climate fluctuations

Our study highlights the importance of the temporal scale considered as the patterns observed differed whether we considered the short- or long-term temporal scale. While a sudden arid event can be beneficial to predator population, increasing aridity over time leads to an overall decrease in predator population size. The explanation of such differences lies in the fact that a predator response over the long term integrates the predator responses over the short-term, along with the long-term response of prey, which declines with increasing aridity (Fig. S9). Therefore, our results illustrate that the long-term response of predator populations to changes in mean annual rainfall cannot be predicted only from the immediate response of predator populations to specific rainfall conditions.

5.4 Considerations on the model

Modelling studies are difficult exercises where one walk on a thin line between complexity/realism and simplification that is required for conceptualization, i.e. building some theoretical understanding. We have tried to do this successfully but we want to underline here a few simplifications made in this study (and already made in classical models of predator-prey interactions – e.g. Wilmers *et al.*, 2007a, b). It is noteworthy that the code of the model is available (<https://github.com/aissamorin/climate-prey-vulnerability-and-predators>) so that one can parametrize it for a specific system and add the complexity that would be considered critical. First, in our model, juvenile prey contribute as much energy as adult prey. Second, the predator population is not age-structured. Third, the predator-prey system modelled here involves one prey and one predator only, yet multi-species assemblages often characterize both prey and predator communities. Predators often prey on several prey species, with primary and secondary prey and display prey switching depending on prey availability and catchability (Owen-Smith & Mills 2008b, Elbroch et al. 2013). The presence of an alternative prey could influence model

outcomes for scenarios 2, 3 and 4: when the vulnerability of the primary prey decreases, if the predator can switch to an alternate prey species available and more vulnerable, the decrease in predator population growth rate or over the long term may be weaker or not observed. In contrast, the presence of competitors preying on the same prey could intensify the decrease in the number of vulnerable prey available to each predator owing to additive effects (Melis et al. 2009), and negatively influence predator population size.

5.5 Conclusion

Despite its general simplicity, this theoretical study highlights the importance of understanding, and accounting for, the vulnerability factors in predator-prey relationships, and sheds light on the complexity of predicting predator-prey relationships in a changing climate. We believe it is a prospective study that suggests interesting future research directions. Based on our work, we advise that future theoretical and empirical works should integrate climate-driven changes in prey vulnerability if we want to grasp the full picture of the impacts of climate changes on predator-prey interactions.

6 Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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8 Author contributions

MV and SC conceived the ideas; AM and SC designed the model. All authors analysed the results, wrote the manuscript, and gave approval for publication.

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10 Data availability statement

The code used for the model and the simulations is available from a GitHub repository: <https://github.com/aissamorin/climate-prey-vulnerability-and-predators>.

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710 **12 Table**

711 **Table 1:** Definitions and values of the state variables and parameters for prey and predators used in the model.

Variables	Definition/description	Values
$N(t)$	Prey population size at the beginning of year t	$N_1=10000$
$J(t)$	Number of juvenile prey at the beginning of year t	$J_1=2500$
$A(t)$	Number of adult prey at the beginning of year t	$A_1=7500$
$Y(t)$	Predator population size at the beginning of year t	$Y_1=10$
$P(t)$	Pool of prey vulnerable to predation for year t	Calculated at each time step
$M(t)$	Pool of prey consumed at the end of year t	Calculated at each time step
α_a	First shape parameter of the Beta distribution from which are drawn adult prey individual survival rate	Calculated at each time step
α_j	First shape parameter for Beta distribution from which are drawn juvenile prey individual survival rate	Calculated at each time step
β_a	Second shape parameter for Beta distribution from which are drawn adult prey individual survival rate	Calculated at each time step
β_j	Second shape parameter for Beta distribution from which are drawn juvenile prey individual survival rate	Calculated at each time step
P_a	Maximum adult prey survival probability	0.95
P_j	Maximum juvenile prey survival probability	0.8
Sd_{pa}	Standard deviation, variation of adult prey survival	0.05
Sd_{pj}	Standard deviation, variation of juvenile prey survival	0.05
g_a	Effect of increased population density on adult survival	$g(N(t)) = \frac{\gamma_{Pa}^{\delta_{Pa}}}{\gamma_{Pa}^{\delta_{Pa}} + \frac{N(t)}{R}}$
g_j	Effect of increased population density on juvenile survival	$g(N(t)) = \frac{\gamma_{Pj}^{\delta_{Pj}}}{\gamma_{Pj}^{\delta_{Pj}} + \frac{N(t)}{R}}$
p_a	Mean adult prey survival probability	$p_a = P_a \times g_a$

p_j	Mean juvenile prey survival probability	$p_j = P_j \times g_j$
γ_{Pa}	Adult half-saturation, point at which adult prey survival is lowered by half	30
γ_{Pj}	Juvenile half-saturation, point at which juvenile prey survival is lowered by half	20
δ_{Pa}	Shape parameter, defines the onset of density-dependence for adult prey	2
δ_{Pj}	Shape parameter, defines the onset of density-dependence for juvenile prey	2
R	Annual level of rainfall	Varies between 300 & 900mm, by 100mm increment
F_{low}	Value determining fecundity value when adult survival is close to 0	100
F_{growth}	Rate at which fecundity value reaches 1	15
Th	Prey threshold of survival probability below which predators can catch and consume the prey.	$Th = 1$ for scenarios 1 & 3; $Th = 0.5$ for scenarios 2 & 4
H_{min}	Lowest value that can be taken by the handling time across all scenarios	5
H_{max}	Highest value that can be taken by the handling time across all scenarios	8
B	Maximum rate of change of the handling time	0.015
V	Rainfall value for which the rate of change of the handling time is maximum (or inflexion point)	600
μ	Encounter rate in the predator functional response	0.0002
h	Predator handling time for one prey in the predator functional response	$h = 5$, for scenarios 1 & 2; h defined by $H = h_{min} + \frac{h_{max}-h_{min}}{1+e^{+B(R-V)}}$, for scenarios 3 & 4
τ	Interference between predators in the predator functional response	0.3
λ_{max}	Predator maximum growth rate	1.8

For herbivore demographic parameters, we chose values that were consistent with values reported in the literature on African large herbivores (e.g. Owen-Smith et al., 1990; Grange et al., 2015). For large carnivore parameters, we chose values that were either consistent with the published literature (e.g. Schaller, 1972), or consistent with our field knowledge of lion and hyaena ecology, or, for parameters that have never been estimated, we adjusted them to allow the model to run and give realistic outcomes.

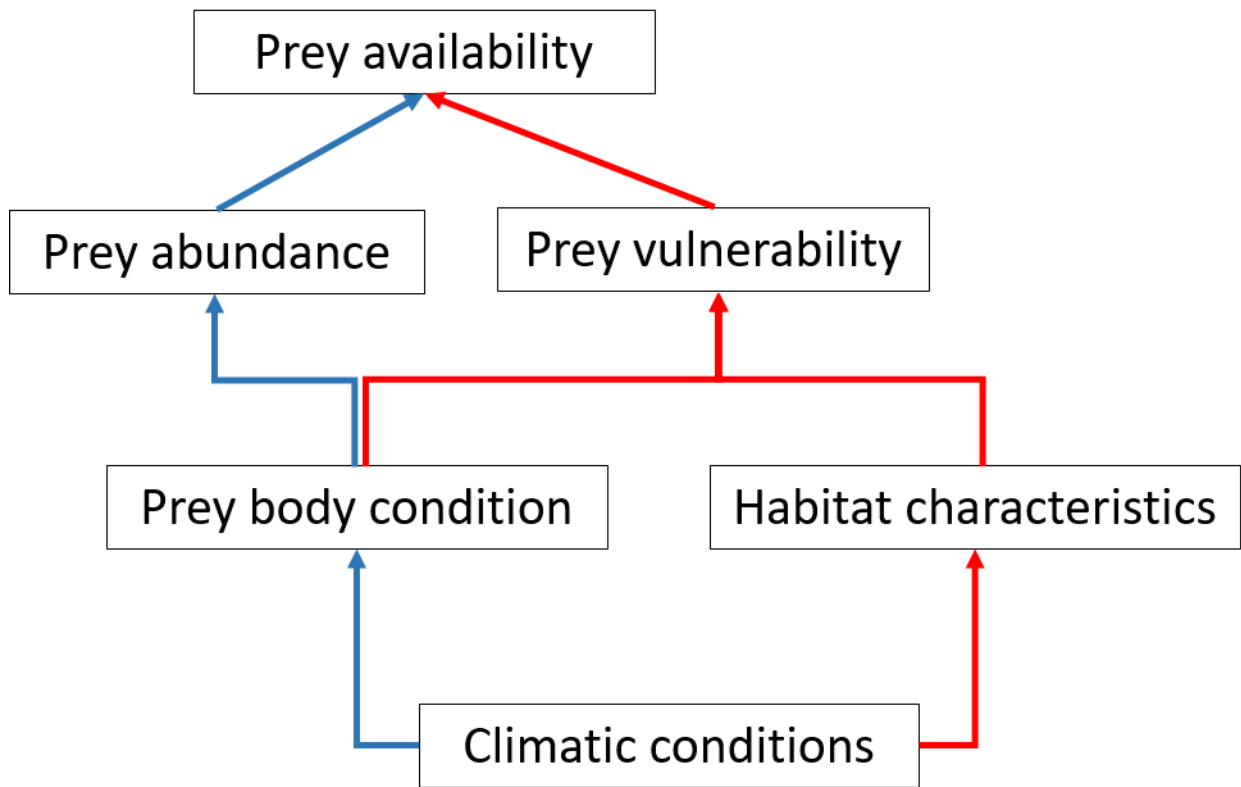
13 Figure captions

Figure 1: The potential pathways by which climatic conditions can affect prey availability for predators. The blue arrows represent the links classically modelled in existing models (scenario 1 in this study). The red arrows represent the links originally modelled in this work (through scenarios 2 to 4).

Figure 2: Summary of the functional relationships underlying the model. (A) Effect of increased number of individuals per resource unit (approximated by rainfall) on mean juvenile and adult prey survival rates adapted from Wilmers et al. (2007b). Mean adult and juvenile prey survival rates have been represented for two values of δ parameter, which controls the onset and the strength of the density dependence. Juvenile prey survival rate has been set to be the first impacted by increasing density. (B) Probability of reproduction as a function of survival probability $p_{ai}(t)$. (C) Functional relationship between rainfall and predator handling time h as defined by eqn. 5 for parameters given in Table 1. The hunting success varies inversely with the handling time.

Figure 3: Model summary with the key model steps. The dashed line arrow symbolizes the next time step. As scenario 1 is independent from vulnerability sources, it is presented aside from the other scenarios. Conversely, details of the processes defining vulnerability related to either body condition or habitat characteristics are presented in scenarios 2, 3 and 4.

Figure 4: (A) Immediate response of predator populations to a specific rainfall condition. Relationship between the growth rate of predator populations and a specific annual rainfall in a system characterized by a long-term mean annual rainfall of 600 mm. (B) Long-term response of predator populations to changes in mean annual rainfall. Relationship between the size of predator populations and long-term mean annual rainfall. While in scenario 1, prey vulnerability to predators did not vary with climatic conditions, in scenario 2, 3 and 4 climatic conditions affected prey vulnerability through, respectively, changes in prey body condition, in habitat characteristics or both. Light-coloured envelopes include minimum and maximum values of predator growth rates (A) or mean predator population sizes (B).



744
745 **Figure 1**

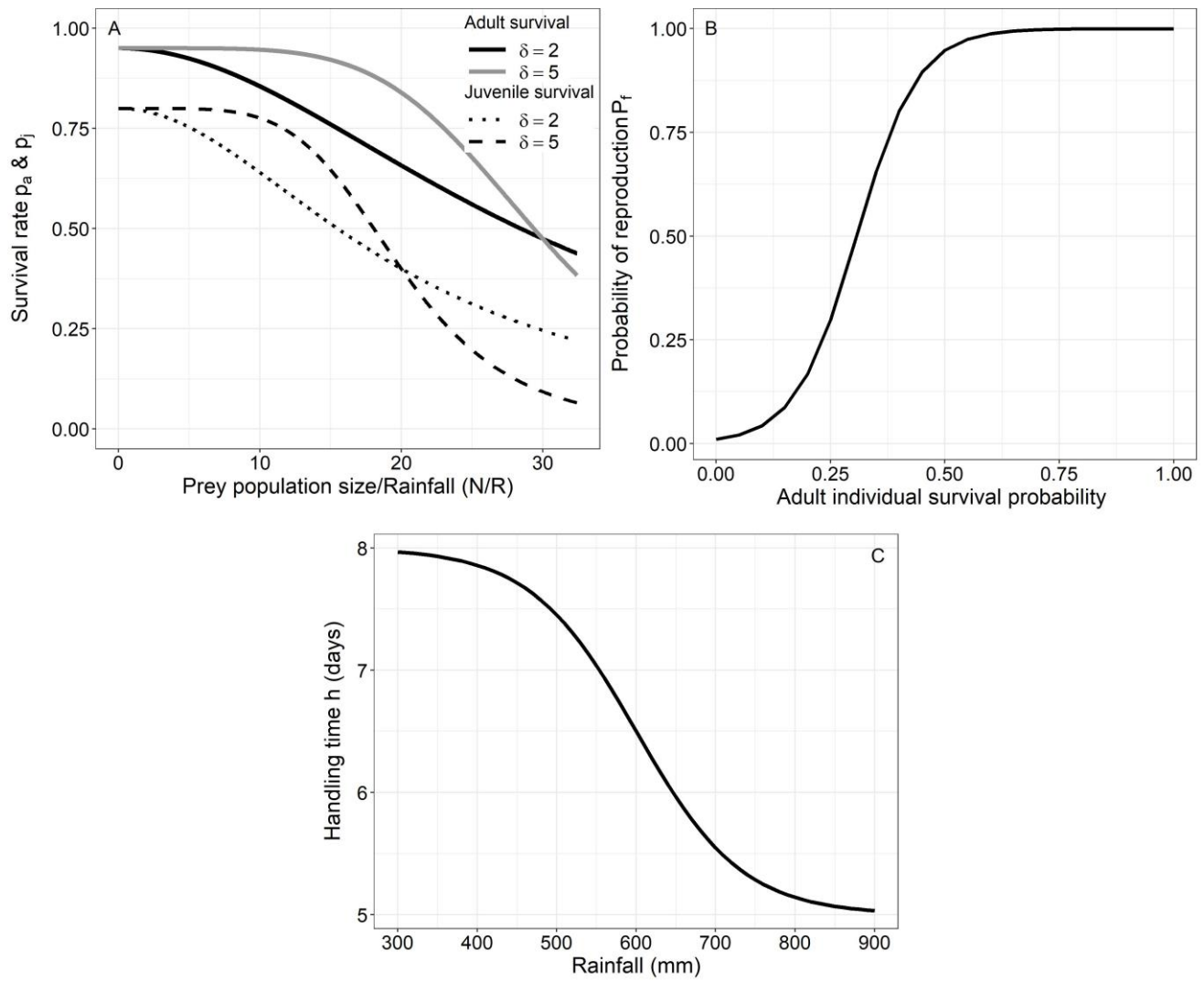


Figure 2

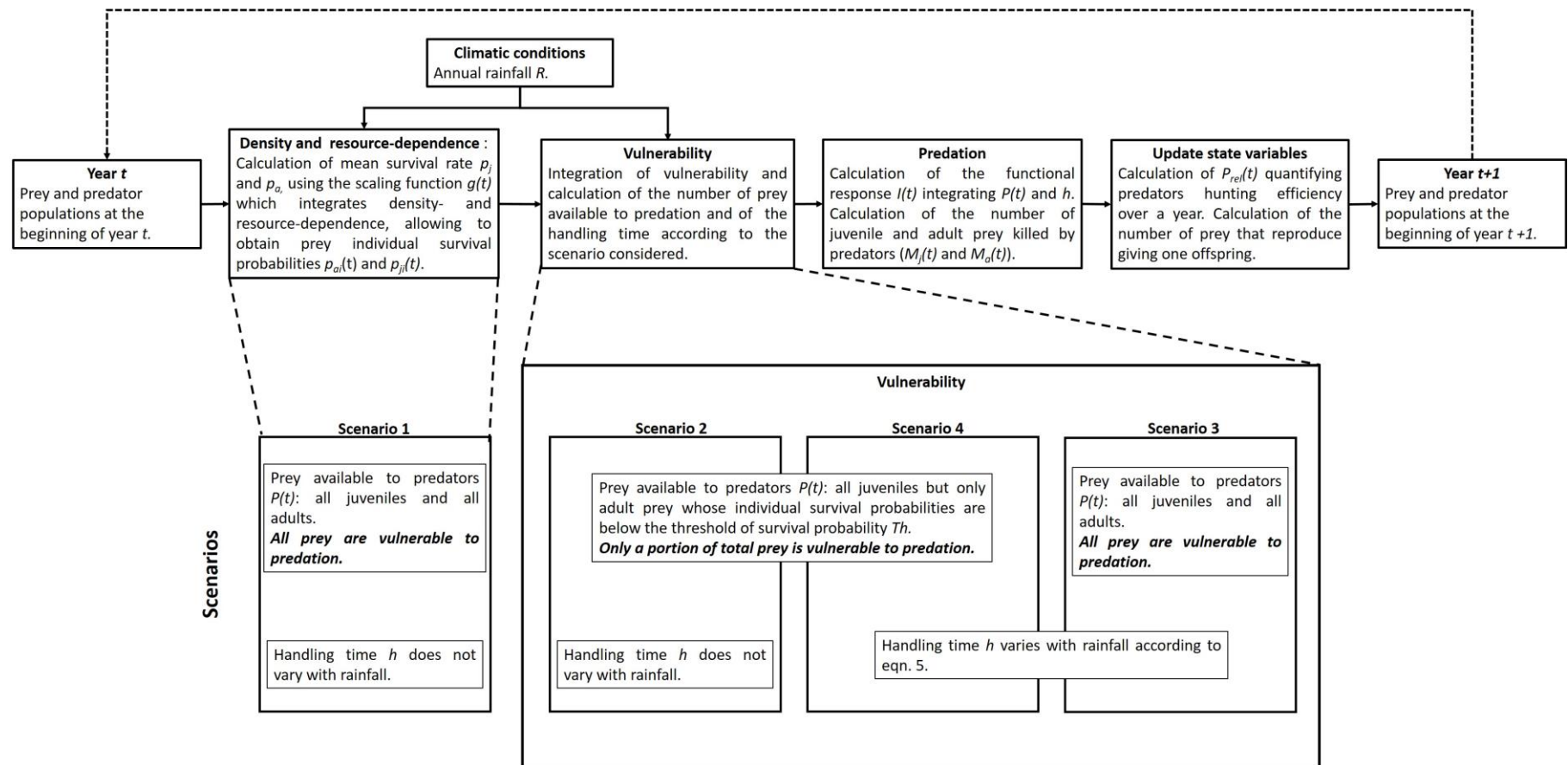
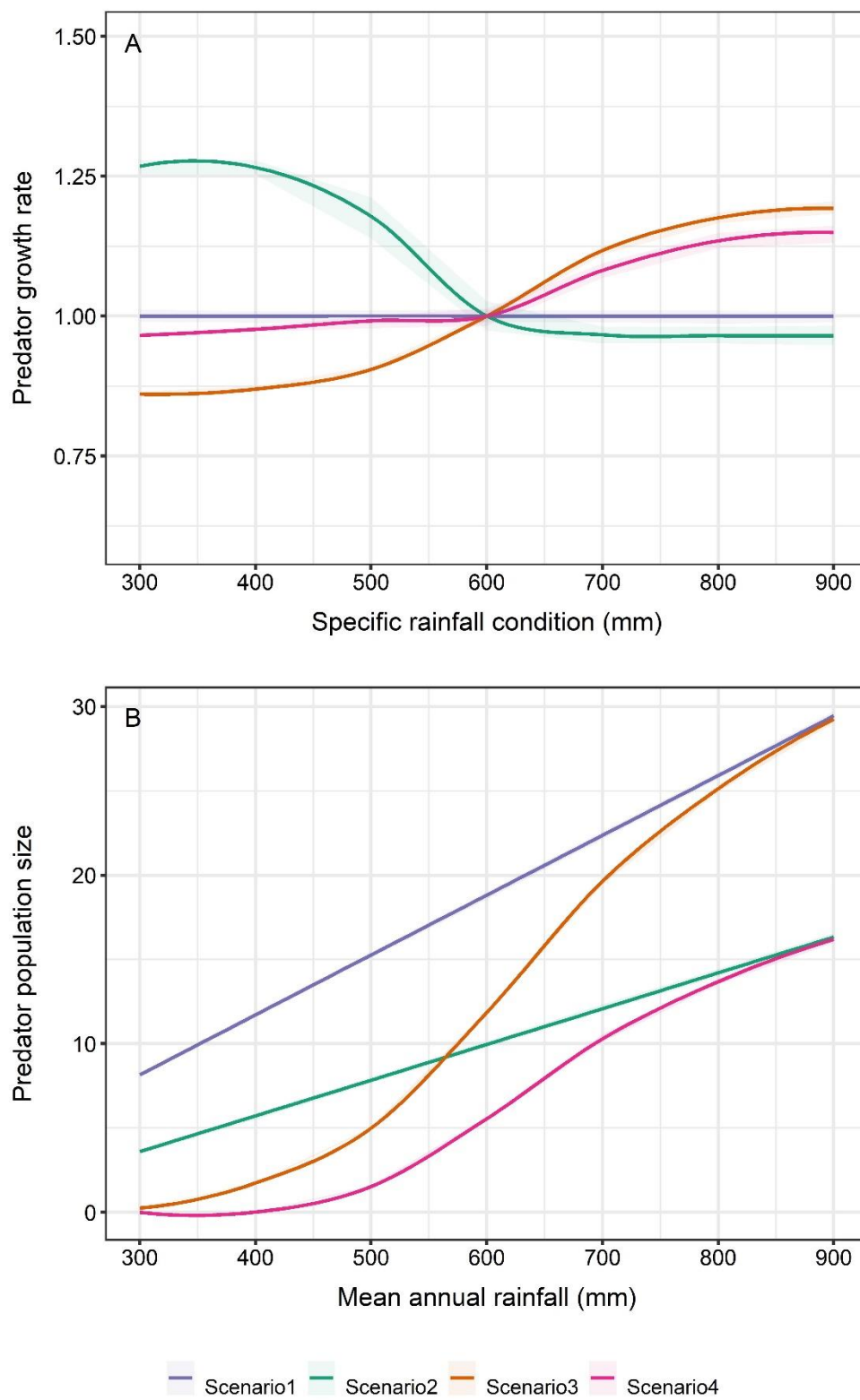


Figure 3



Supplementary Material

1 Appendix A: Responses of predator populations to an increase in rainfall when habitat driven hunting success decreases with rainfall

1.1 Context

The results presented in the main manuscript only accounted for a positive relationship between predator hunting success and rainfall which is expected in semi-arid ecosystems such as savanna. Hereafter, we present the methods, results and sensitivity analyses for systems characterized by the alternate relationship with hunting success decreasing as rainfall increases.

1.2 Materials and methods

The predator-prey model is the same as the one presented in the main manuscript. In this alternate situation, we again integrated the influence of habitat characteristics that could affect prey vulnerability through the manipulation of the handling time h . However, here we assumed that handling time h would increase with rainfall and that higher rainfall levels would correspond to higher h values and consequently longer times to subdue one prey, i.e. decreased hunting efficiency and success than at lower rainfall levels (Fig. S1). Therefore, h varies with rainfall according to the following equation:

$$H(R) = h_{min} + \frac{h_{max} - h_{min}}{1 + e^{-B(R-V)}} \quad (1)$$

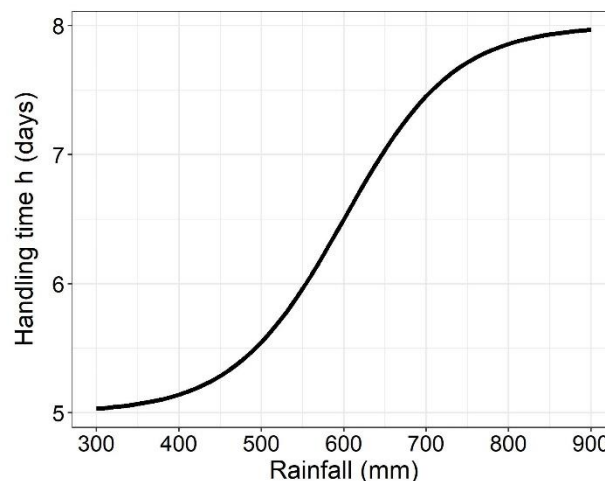


Figure S1: Functional relationship between rainfall and predator handling time h as defined by (1). The hunting success varies inversely with the handling time. For parameters see Table 1 of the main manuscript.

1.3 Results

1.3.1 Immediate response of predator populations to specific rainfall conditions

When climatic conditions influenced prey abundance only (scenario 1), the population growth rate of predators was not influenced by the specific climatic condition of the year (Fig. S2A). In contrast, in the three other scenarios, the population growth rate of predators in one year was influenced by the specific climatic condition of the year. Predators from the three scenarios, benefited from below-

average rainfall (600mm) and their populations increased, but were negatively impacted by increasing rainfall (Fig. S2A). Finally, unlike the results presented in the main manuscript, the combination of vulnerability effects in scenario 4 made this scenario the one with the most extreme responses, and predator growth rates were negative at above-average rainfall and positive at below-average rainfall (Fig. S2A).

1.3.2 Long-term response of predator populations to changes in mean annual rainfall

Over the long term, our results show here again an effect of mean annual rainfall on the size of predator populations for all scenarios. Scenario 1 and 2 show similar patterns as those presented in the main results, as the size of predator populations increased near-linearly with rainfall for both scenarios and scenario 2 being characterized by lower predator population size than scenario 1. The size of predator populations in scenario 3 and 4 also varies non linearly, displaying a unimodal response to increasing rainfall. In scenario 3, the size of predator population first increased with increasing mean annual rainfall, before decreasing (Fig. S2B). The size of predator populations in scenario 3 were greater than those from scenario 2 up until mean annual rainfall reached values around 600mm, but were smaller for values above (Fig. S2B). The size of predator populations from scenario 4 varied virtually identically as in scenario 3 with rainfall but with lower values of predator population sizes (Fig. S2B).

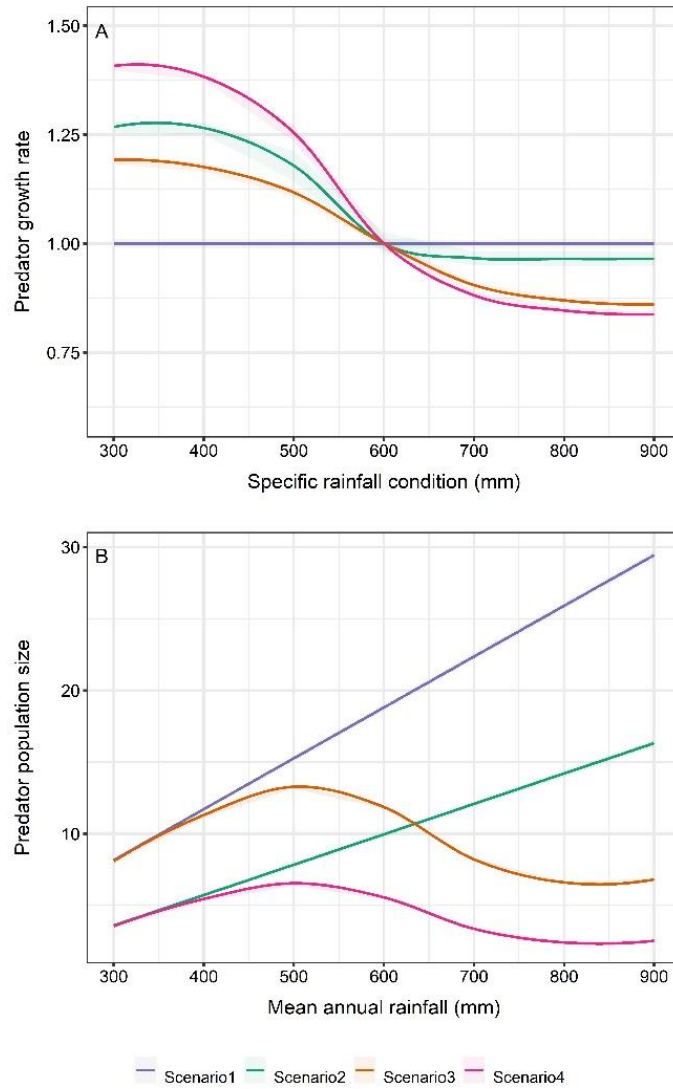
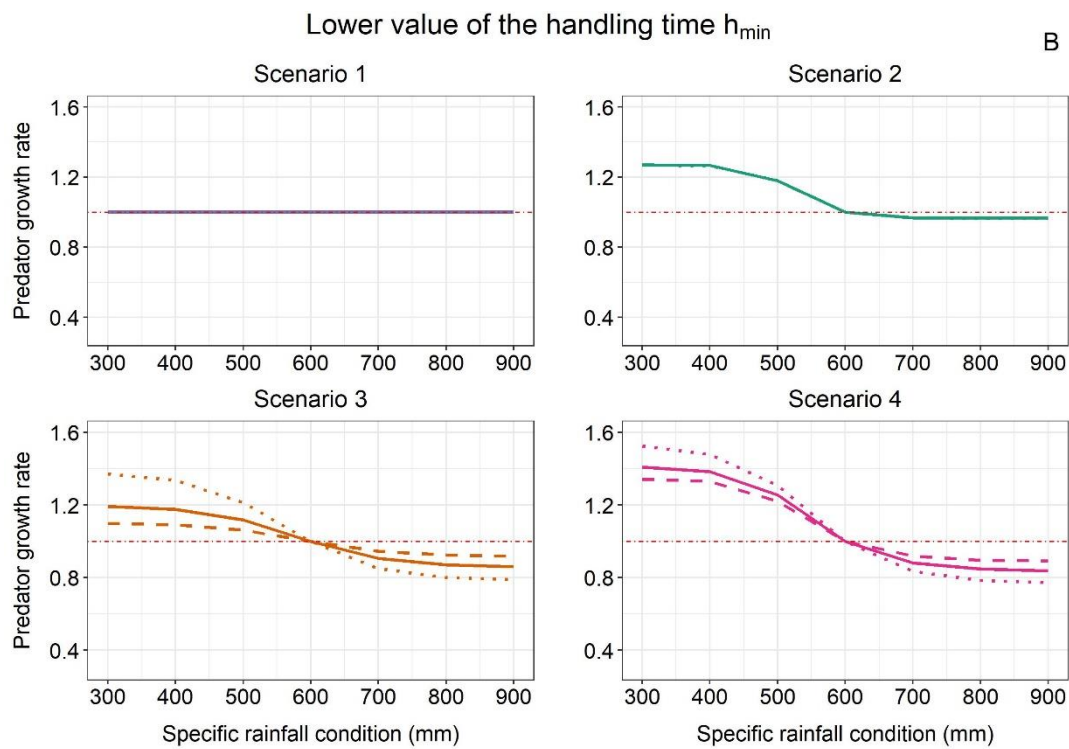
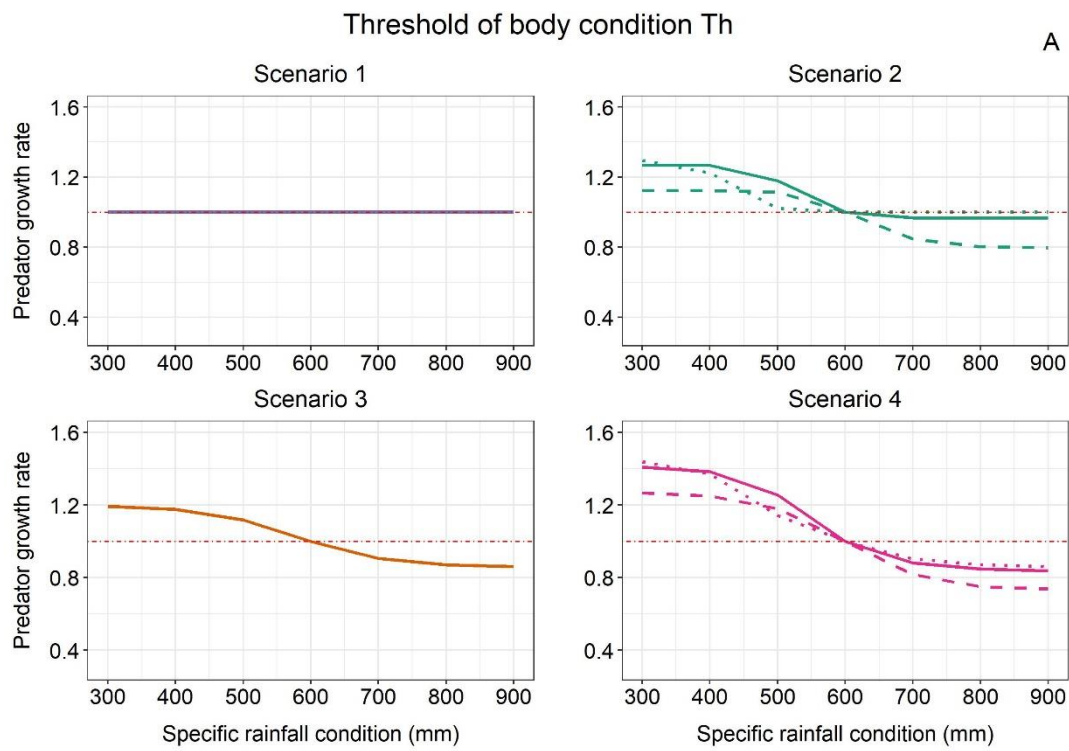


Figure S2: (A) Immediate response of predator populations to a specific rainfall condition. Relationship between the growth rate of predator populations and a specific annual rainfall in a system characterized by a long-term mean annual rainfall of 600 mm. (B) Long-term response of predator populations to changes in mean annual rainfall. Relationship between the size of predator populations and long-term mean annual rainfall. Light-coloured envelopes include minimum and maximum values of predator growth rates (A) and mean population size (B).

1.4 Sensitivity analyses

Sensitivity analyses of the immediate response of predator to 20% change in parameters when the habitat-driven hunting success decreases with rainfall.



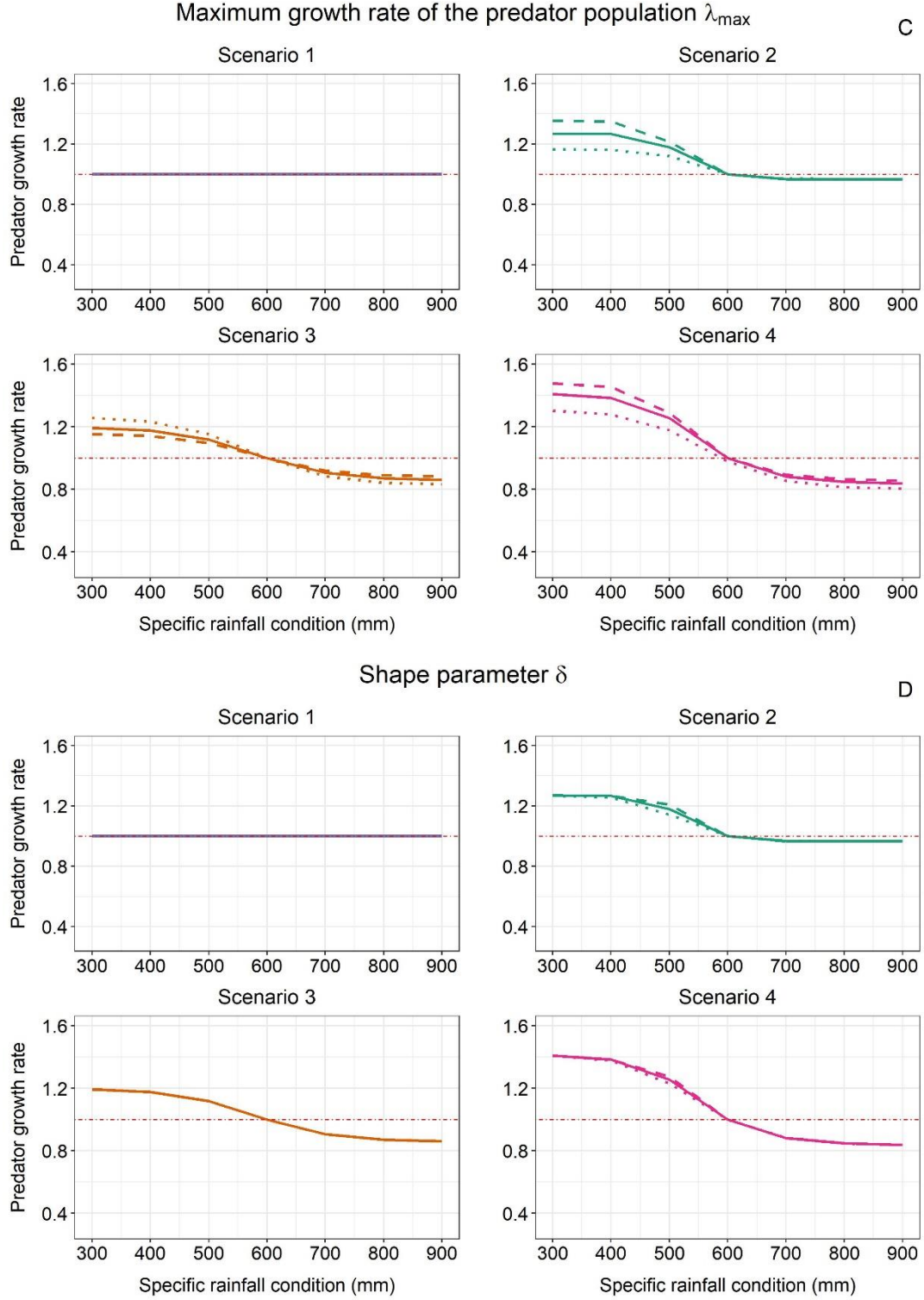
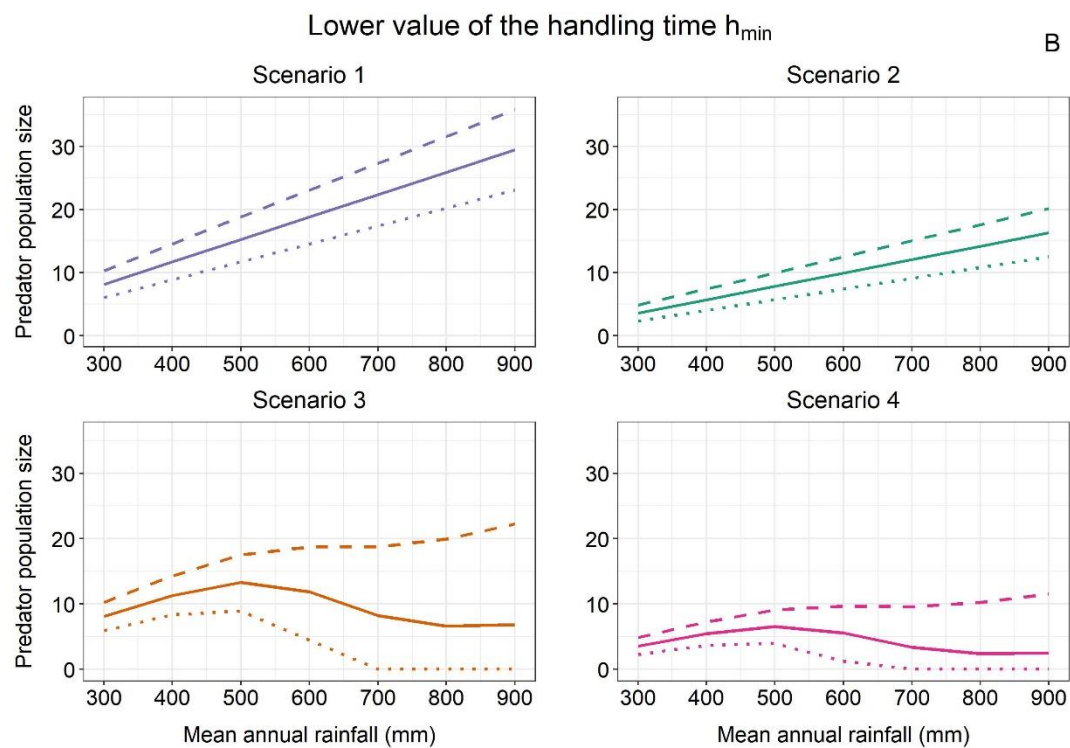
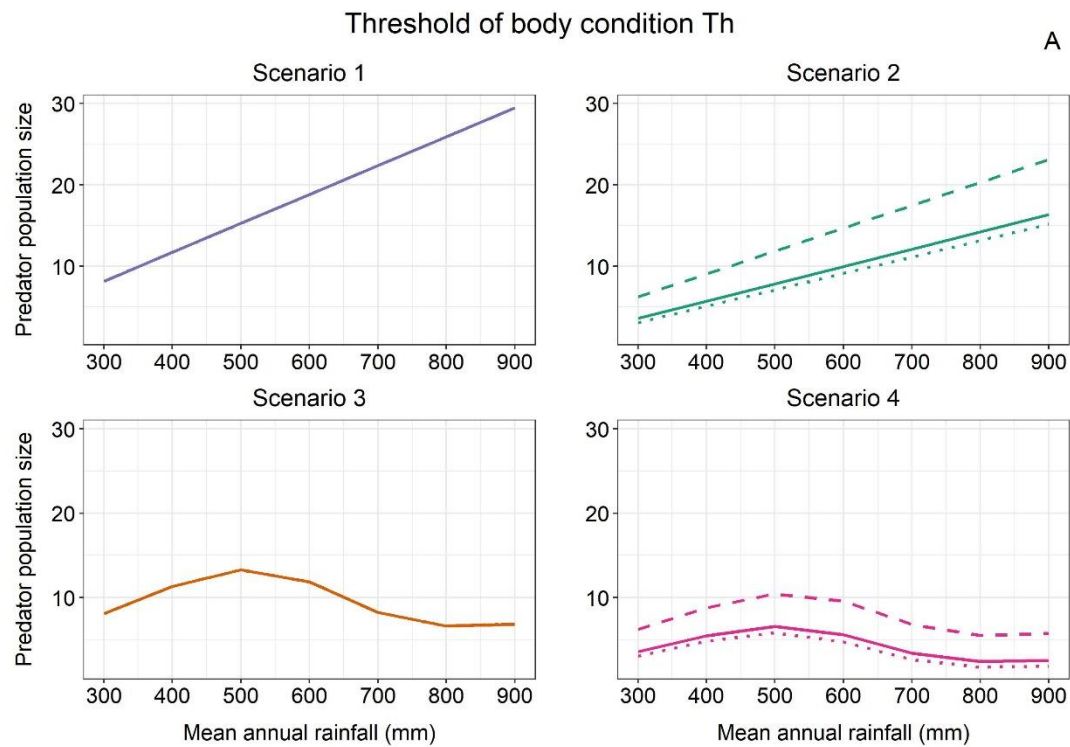


Figure S3: Influence of a specific rainfall condition on the growth rate of predators from the four scenarios for three values (default: solid line, + 20%: dashed line, -20%: dotted line) of tested parameters: (A) Th , (B) h_{\min} , (C) λ_{\max} , (D) δ , when the habitat-driven hunting success decreases with rainfall. All other parameters are set to default values. Red dotted lines correspond to a predator growth rate equal to 1.

Sensitivity analyses of the long-term response of predators to 20% change in parameters when the habitat-driven hunting success decreases with rainfall.



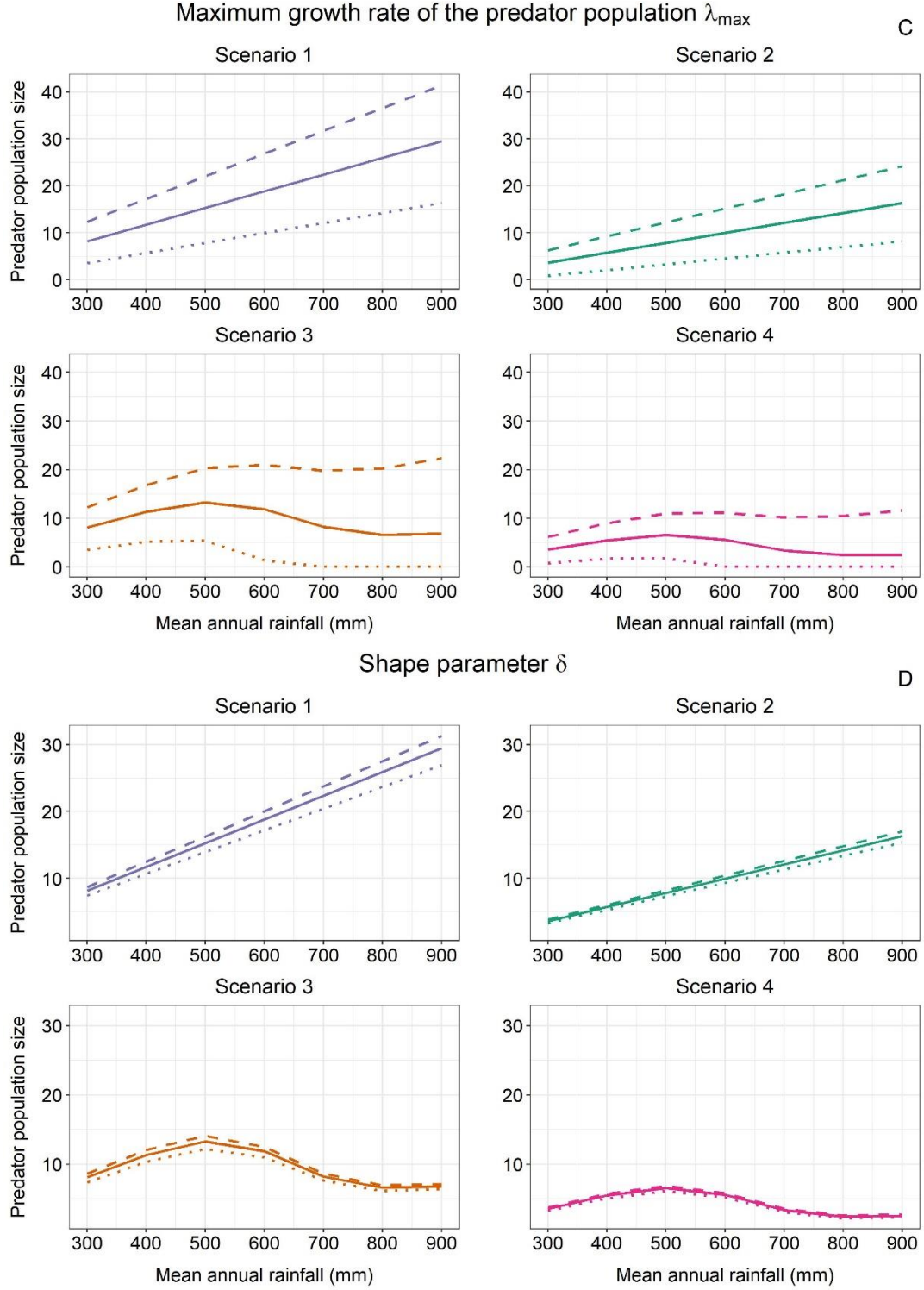


Figure S4: Influence of long-term mean annual rainfall on the size of predator populations from the four scenarios for three values (default: solid line, + 20%: dashed line, -20%: dotted line) of tested parameters: (A) Th , (B) h_{\min} , (C) λ_{\max} , (D) δ , when the habitat-driven hunting success decreases with rainfall. All other parameters are set to default values.

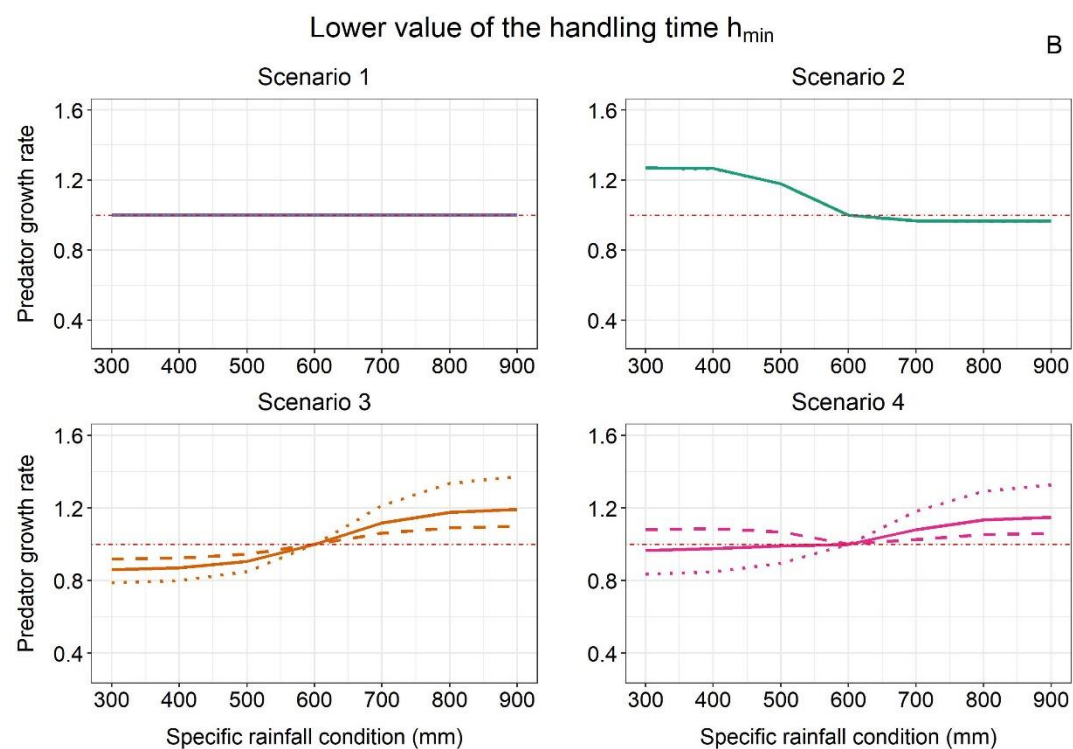
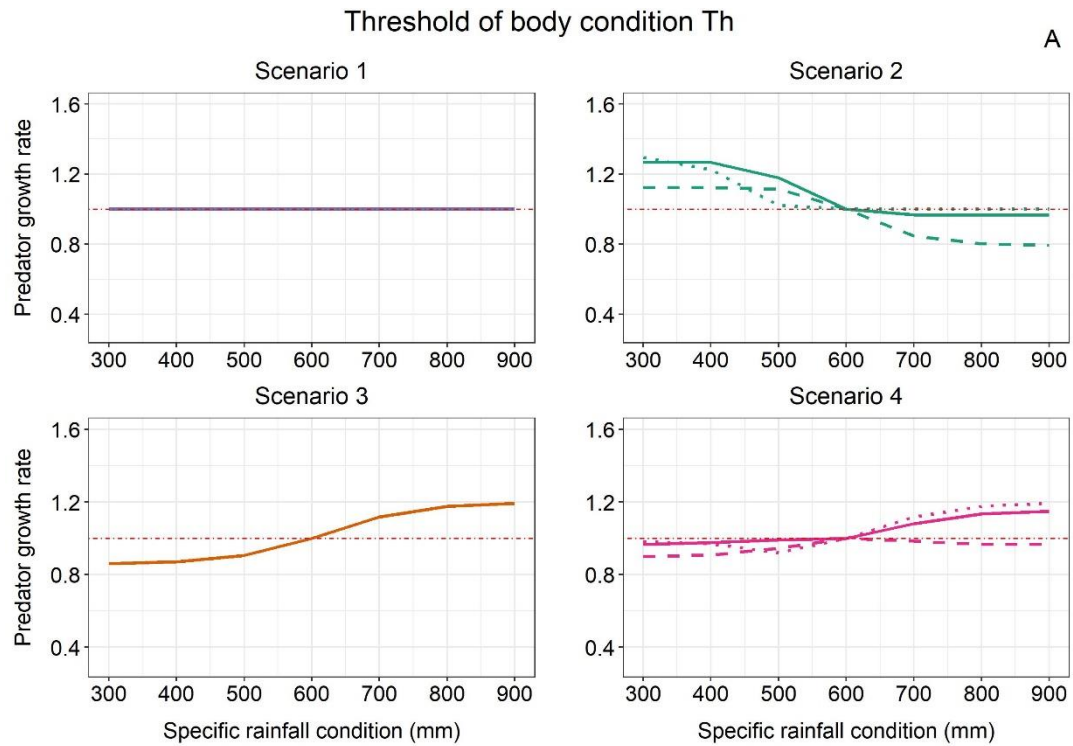
2 Appendix B: Sensitivity analyses

2.1 Results of sensitivity analyses

Sensitivity analyses showed that the results observed were robust to changes in the 4 study parameters as decreasing or increasing parameter values by 20% mostly triggered quantitative rather than qualitative changes in the patterns compared to those displayed for default values (Figures S5 and S6). However, we can note that when we increase Th by 20% for scenario 4 (Figure S5A), the predator population growth rate remains below 1 for high values of rainfall contrary to our expectation. However, it remains greater than the growth rate observed for lower values of rainfall. Additionally, other particular cases arise when we increase λ_{max} and h_{min} by 20% for scenario 4 (Figures S5B and S5C), for small rainfall values. The explanation probably lies in the fact that λ_{max} and P_{rel} , which contains h_{min} in its denominator as shown by *eqn. 11*, are both included in *eqn. 10* but reached values too high for the effect of prey populations on predators to be still detectable in comparison to the rate of increase of predator population. This allowed the rate of increase to remain positive and predator populations to increase.

2.2 Figures

Sensitivity analyses of the immediate response of predators to 20% change in parameters.



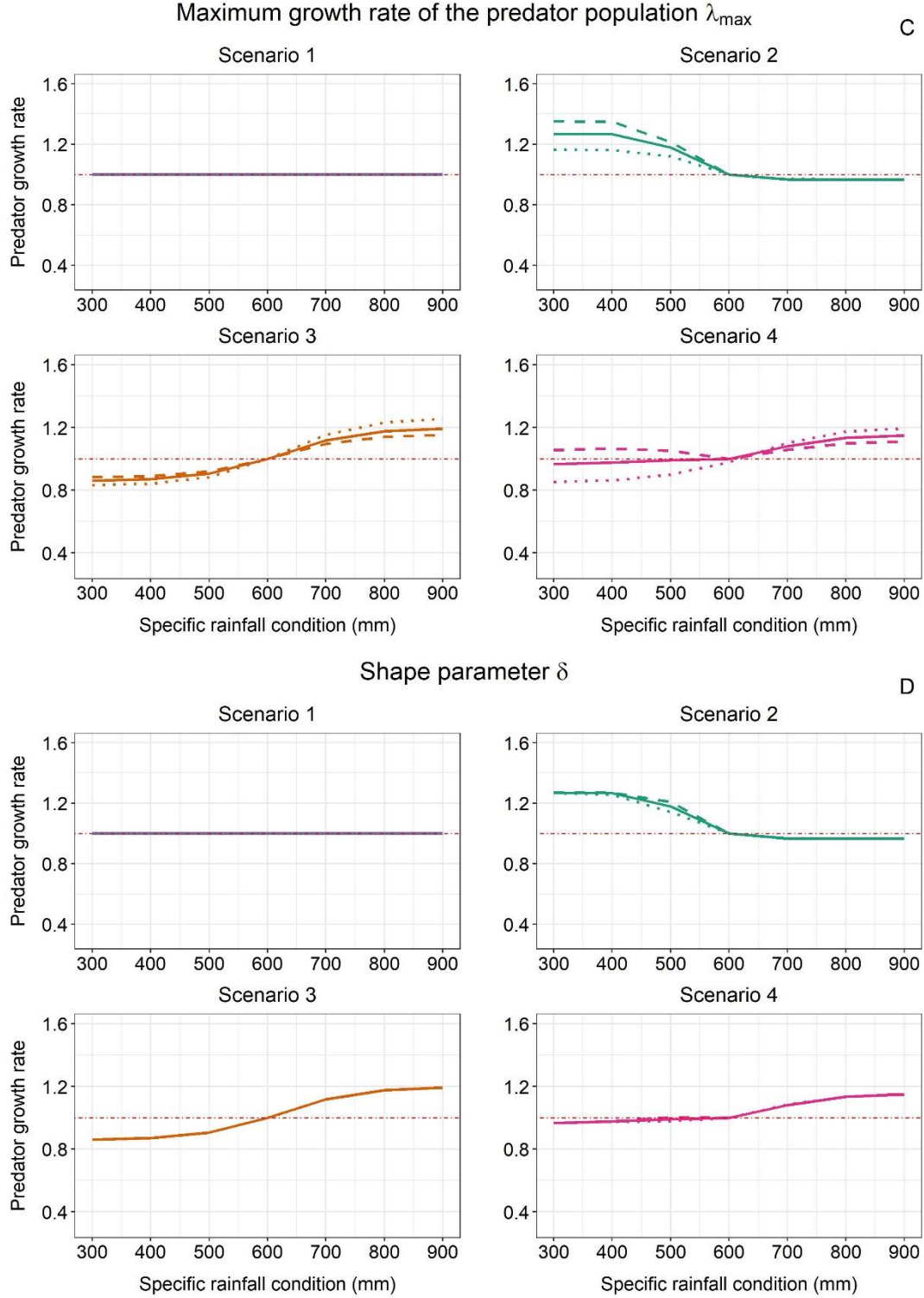
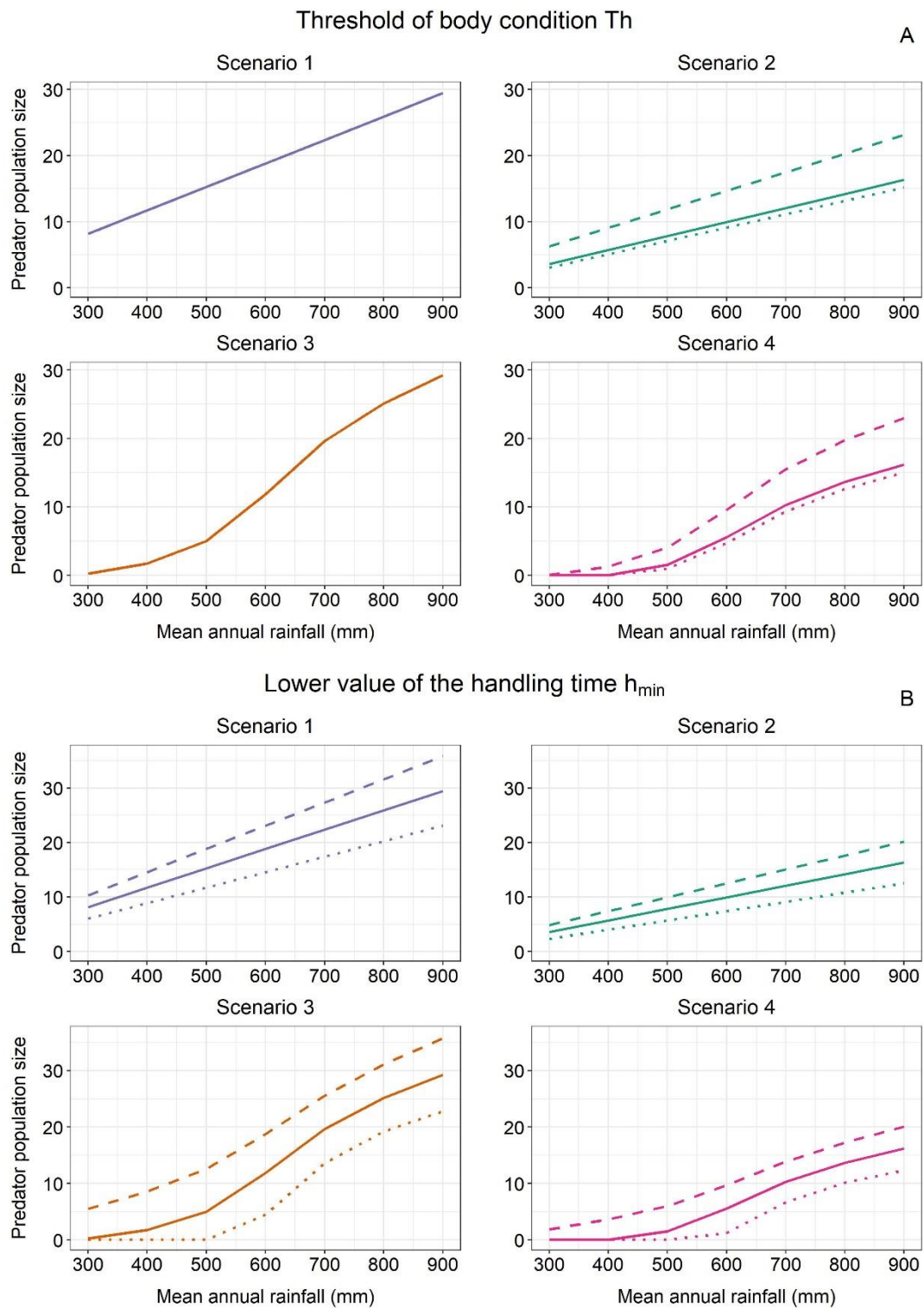


Figure S5: Influence of a specific rainfall condition on the growth rate of predators from the four scenarios for three values (default: solid line, + 20%: dashed line, -20%: dotted line) of tested parameters: (A) Th , (B) h_{\min} , (C) λ_{\max} , (D) δ . All other parameters are set to default values. Red dotted lines correspond to a predator growth rate equal to 1.

Sensitivity analyses of the long-term response of predators to 20% change in parameters.



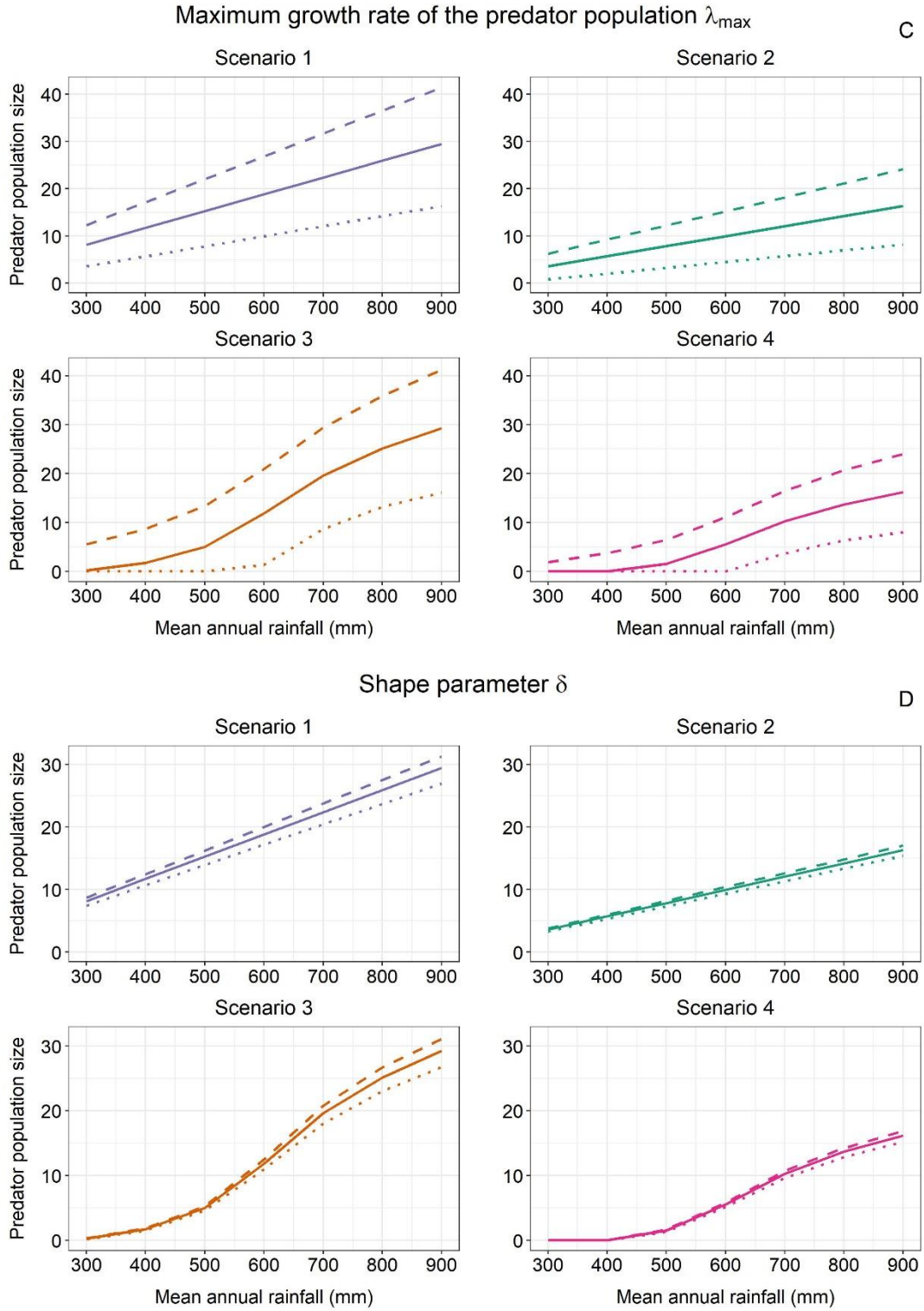


Figure S6: Influence of long-term mean annual rainfall on the size of predator populations from the four scenarios for three values (default: solid line, + 20%: dashed line, -20%: dotted line) of tested parameters: (A) Th , (B) h_{\min} , (C) λ_{\max} , (D) δ . All other parameters are set to default values.

3 Appendix C: Supplementary figures

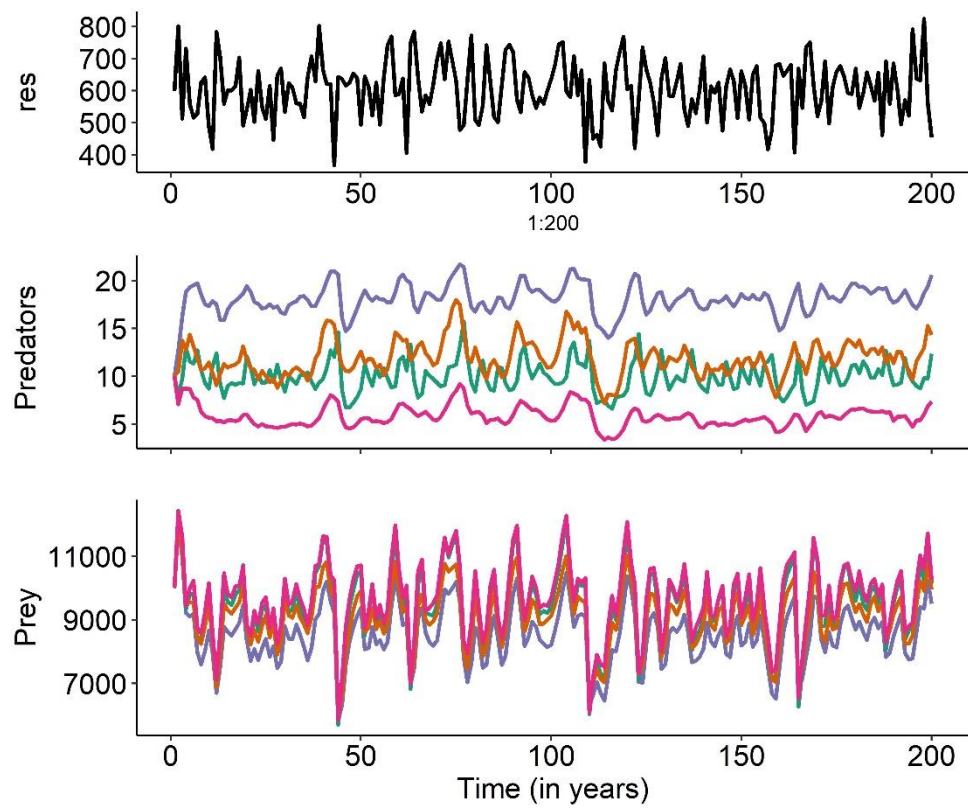


Figure S7: Model behaviour for one run. Rainfall (top), predator (middle) and prey (bottom) population sizes, for a 200-year run. Used parameter values are presented in Table1.

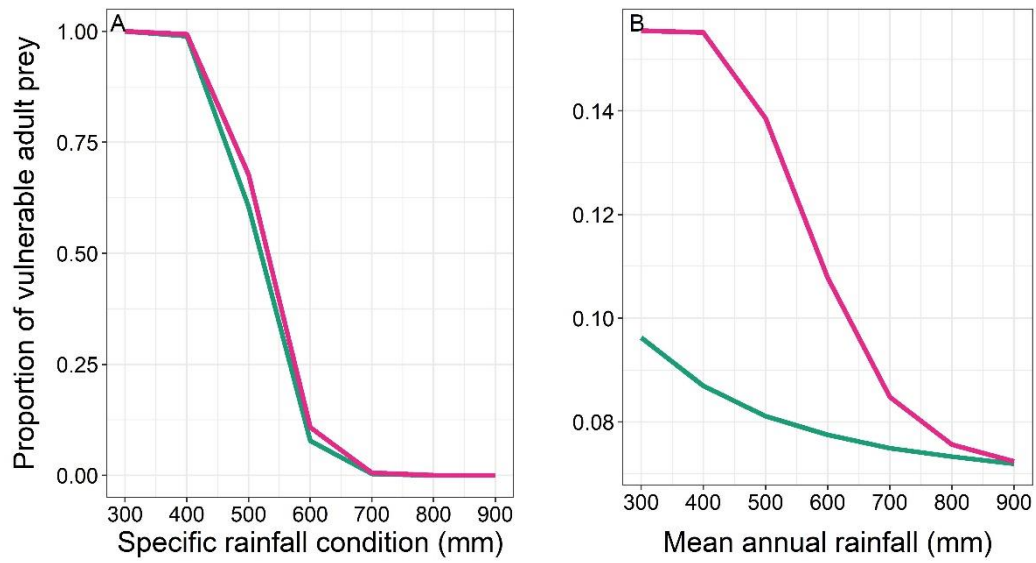


Figure S8: (A) Influence of a specific rainfall condition on the proportion of adult prey vulnerable to predators in scenarios 2 (green) and 4 (pink). (B) Influence of mean annual rainfall on the proportion of adult prey vulnerable to predators in scenarios 2 (green) and 4 (pink). By definition the proportion of adult prey for predators from scenarios 1 and 3 is set to 1.

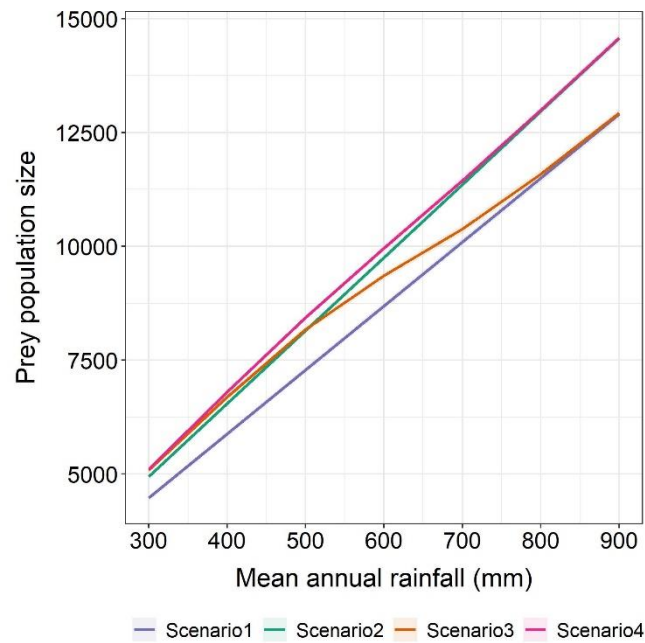


Figure S9: Influence of mean annual rainfall on the size of prey populations, for the four scenarios.